

ARCHITECTURE OF TROPICAL PLANTS

P. B. Tomlinson

Harvard Forest, Harvard University, Petersham, Massachusetts 01366

INTRODUCTION

This article deals with an apparent paradox, a reductionist approach that allows the seeming chaos of forest canopies to be seen as a sequence of simpler processes but that retains an appreciation for holistic aspects of plant construction. Tropical forests offer the biggest challenge to such an approach because the chaos is acute.

The idea of looking at the total developmental organization, or architecture, of tropical trees has taken a surprising time to mature. For example, the first description of *Terminalia catappa*, a common coastal tree of the Asian tropics, included an accurate representation of its distinctive physiognomy (76), which has been frequently referred to in the literature as the *Terminalia*-habit (17, 43,). However, 300 years passed before a quantitative analysis of the habit was made (29). This neglect of total form has resulted primarily from the necessity of describing and diagnosing woody plants from herbarium specimens that can represent a species only fragmentarily. Nevertheless, total organization is increasingly seen as important in understanding ecological and demographic processes, because a plant reacts with its environment as a whole, and its demography involves not merely the genetic individual but the individual as established by modular construction—the deployment of a variable set of meristems capable of indefinitely repeating a hierarchy of parts. Modular organisms of this kind therefore have enormous phenotypic plasticity (103); recognizing an underlying pattern may be difficult.

The study of plant architecture can therefore be seen as a recent development in plant morphology but one with close connection to other fields (30, 32, 92). It was formally initiated by Hallé & Oldeman in 1970 in a study of

tropical trees, later to be elaborated and presented in an ecological context (44). *Architecture* is defined as the visible but momentary expression of tree form and is based on the concept of the architectural model, an abstraction that refers to the genetically determined growth plan of the tree. The relationship is like that between a blueprint and the structure built from it. Unlike a blueprint the concept is dynamic, because a tree has an extended elaboration in time as well as in space. Parameters involved in the analysis of form include: contrasts between rhythmic and continuous growth; secondary changes in orientation; branch distribution, differentiation and orientation; and position of inflorescences. Many of these features can be observed only by studying the tree for extended periods of time. Morphological information can often be interpreted dynamically, however, as when evident articulations in shoot morphology result from episodic growth increments. Root systems are much less well analyzed because of their inaccessibility (50). Only in mangrove plants, which usually have well-developed aerial portions to their roots, is there extensive information about the dynamics of root construction (93, 96; but see also 60). Architectural analysis was developed in the tropics because tree form is most diverse in regions with minimal or no differences between seasons; the diversity of species there is greatest, and the range of growth expression largest. One can, for example, only achieve the full range from continuous to rhythmic growth in a nonseasonal climate. Ng (65) provides examples from the Dipterocarpaceae. Episodic growth may then be the result of internal feedback mechanisms (8).

Hallé et al provided a set of 23 architectural models (each named after a botanist who had contributed to an understanding of the total form of woody plants); they recognized that many trees from unrelated families showed similar overall organization. The approach was entirely empirical. Hallé et al emphasized that the diversity of deterministic tree forms constituted a continuum within which their models formed descriptive points of reference, around which many taxa could be grouped. The value of the system is the precision brought to the understanding of seemingly chaotic diversity. An important extension of this descriptive approach was the recognition that individuals may or may not conform precisely to a given architectural model (68). Species can express their growth model precisely, as in palms and many conifers, but most trees are subject to environmental disturbance to which they respond by some reiterative ability, i.e. a repetition of all or part of the growth model. This plasticity may be as significant as the original architecture in interpreting the adaptive response of a species to ecological variables; it leads to the generalized concept of deterministic and opportunistic processes in plant construction (91). Reiterative ability itself is capable of some kind of categorization depending on the stimulus that induces opportunistic development (13). This duality between architecture and reiteration has rarely been

considered by morphologists who have been largely preoccupied with essentialistic notions of organization, but it is seen to be important in demographic analysis (e.g. 61, 62). The evolutionary significance of plasticity of plant form also remains little investigated. Distinguishing opportunistic from deterministic processes may itself be a subjective process (e.g. 40) and may involve seemingly minor switches in developmental control, as discussed later.

Architectural analysis is, of course, applicable to all organisms with modular construction. An example is in the study of rhizomatous plants, which have precise branching patterns in a single plane, so that rather exact shoot geometries can be recognized in different species (3, 5, 7). These plants may thus optimize an exploration of a mosaic of nutrient or light resources. Where the intrinsic geometry is not obviously regular, stochastic rules for generating colonizing patterns can still be extracted (74, 75).

Clearly a restriction of a discussion of architecture to tropical plants or plants of one growth habit is artificial, but the subject becomes unwieldy if it is not constrained. In this review I deal with developments in certain fields that have been influenced by the concept of architecture, and I refer mainly to literature subsequent to Hallé et al (44), which provides the most useful introduction to the subject. To broaden the discussion I also touch upon quantification, emphasize the important contributions being made by paleobotanists, and suggest that architecture is a field of interest to developmental biologists. I draw on nontropical examples where necessary but largely restrict the discussion to trees.

Variation Within a Single Individual

In its simplest expression, the architectural model implies that a tree grows by the elaboration of a set of basic rules that remain unchanged with age, but this assumption needs more detailed discussion. The abstract model can only be recognized by observing the total development of an individual in time, although comparison of different-aged individuals—either within field populations, in plantations, or in an arboretum—can provide short cuts to a full analysis. Analysis is still difficult because a tree may or may not grow according to an existing named model. The architectural model is also phenotypically plastic. The first problem may be resolved by introducing the idea that a given species may combine elements of a number of contrasted (but often developmentally related) models (30, 40, 45, 46). Sometimes this plasticity can be ascribed to an irregularity in the development of the tree itself, as in *Tsuga* where the trunk axis is consistently neither sympodial nor monopodial in its branching (46). Axis organization within an individual can vary between strict orthotropy and strict plagiotropy, even though closely related models may be defined as having one or the other kind of orientation.

Otherwise, trunk formation can fluctuate between parameters that define contrasted architectural models, as in *Neea* (Nyctaginaceae, 40).

More precise changes can indicate a regular ontogenetic switch during the development of the tree, which otherwise may go unobserved in limited ontogenetic study. Hamilton (45) designated three types of branching (his 1-3) in lateral axes of *Psychotria* (Rubiaceae), each of which defines an entire tree in the Hallé-Oldeman system. He noted changes in branching type, as an architectural feature, in contrasting trunk and higher order axes. *Tabebuia rosea* (Bignoniaceae) changes from symmetric to asymmetric bifurcation after about five orders of branches are produced and then undergoes a regular repetition of this two-phase growth plan as the crown develops, since a new trunk axis is regenerated at intervals (11). In this, and many other species, the distinction between what is architecture and what is reiteration is not clear, as if plasticity of architecture were built into the model itself (cf 40). This process especially characterizes those models with mixed axes (models of Troll, Champagnat, and Mangenot) which are correspondingly difficult to recognize. Plasticity is here expressed as regular changes of orientation within a single shoot (mixed axis—see also 70).

In a study of several trees from the Asian tropics with monopodial architecture the concept of "architectural metamorphosis" during tree development was introduced by Edelin (21). This involves the intercalation of axes of a characteristic orientation into the growing crown at progressively higher branch orders. Thus, a first order (ax_1) branch low in the crown may have horizontal orientation, but at a higher level an ax_1 can show an oblique orientation. Horizontal orientation is now restricted to the next higher branch order (ax_2) on this ax_1 . This can continue as higher orders of branches (ax_3 . . . etc) are produced. This metamorphosis is particularly characteristic of Dipterocarpaceae and may lead to the recognition of different architectural models at different stages of tree development (1, 42). The biological implications of these changes are ecologically profound since they suggest that the crown form adapts to microclimatic changes at increasing heights. A comparable phenomenon is the change in reiterative ability with age, which is sometimes correlated with the more generalized morphological change from juvenile to adult morphology. In *Rhizophora*, for example, there is a marked propensity for adventitious development of shoots in seedlings (an example of reiteration, e.g. 41, 58). In adults, however, reiteration is almost exclusively from dedifferentiation of existing axes; crown form involves virtually no activation of dormant meristems.

A similar transition can occur in conifers, and *Phyllocladus* provides an extreme example in which the adult axes produce no reserve meristems because shoot development is totally preoccupied by flattened leaf-like branch complexes (phylloclades). All true leaves are reduced to nonphotosynthetic

scales that subtend no axillary meristems. Adult *Phyllocladus* can be said to combine elements of the models of Massart, Cook, and Roux (Tomlinson, unpublished, cf 21). Reiteration of adult trees is only possible by de-differentiation of existing axes. However, in seedling axes that support juvenile needle-like foliage leaves (presumably ancestral), but initially no phylloclades, direct generation of new trunks (orthotropic axes) does occur from dormant axillary meristems. This regenerative ability is important ecologically since it can be part of the fire resistant properties of some populations (F. Podger personal communication). Fink (27, 28) has recently discovered that many conifers produce minute undifferentiated detached meristems in the leaf axil. These can be important in shoot regeneration. This observation underlies the value of continued study of shoot anatomy in plants; it connects architecture to ecology in a very direct way. The distribution of these meristems varies in a species-specific way (12).

Architecture in Systematics and Phylogeny

For practical reasons a herbarium study of plants is limited to the examination of fragments and is concerned minimally with development. Architectural analysis is strongly field oriented since it deals with the whole tree, but with its emphasis on dynamics and vegetative features, it can make a systematic description more complete and may provide new characters for diagnostic purposes. The family Rubiaceae has been investigated particularly well in this respect (2, 26, 45, 71, 88). In turn, this information can help in the identification of sterile material. Architectural knowledge may give a better idea of what part of a plant has been sampled in assembling the herbarium specimen and can eliminate confusion between samples of one plant in juvenile and adult phases, which are sometimes interpreted as belonging to different species. Description may be made more complete if the difference between leaf arrangements on orthotropic and plagiotropic axes is appreciated. Many representatives of the models of Massart, Cook, and Roux have contrasted phyllotaxis (distichy vs spiral) on differently orientated axes. Taxonomic description, however, usually refers only to the former because flowers may be restricted to plagiotropic axes. The collector should be encouraged to include contrasted types of axes when making specimens, even though orthotropic axes are sometimes sterile. Refinement of phyllotactic knowledge can improve systematics. *Anisophyllea disticha* (Anisophylleaceae) is distinct from all other flowering plants in the unique tetrastichous phyllotaxis of its plagiotropic axes (98). The same phyllotaxis may characterize the whole genus. This is but one of a suite of characters that distinguishes Anisophylleaceae from Rhizophoraceae, two families traditionally united (51).

Some earlier systematic literature is a good source of architectural information; several Hallé-Oldeman models are named after systematists in

recognition of their unusually complete taxonomic descriptions, e.g. Fagerlind (26), Leeuwenberg (59), Petit (71), Stone (87). Donoghue (19) demonstrates that major sections of *Viburnum* (Caprifoliaceae) can be diagnosed by their contrasted architectures. In the Rubiaceae, Hamilton (45) has extended Fagerlind's work on *Randia* to *Psychotria*. All species studied had a consistent architecture that was diagnostic for certain subgenera and species groups, but which often combined features otherwise separated in the Hallé-Oldeman system. Architectural analysis can emphasize basic differences in organization between major groups. Thus, palms, cyclanths, and pandans, though traditionally juxtaposed in classification of monocotyledons, are fundamentally dissimilar in inflorescence position, branching, rooting, and regenerative ability. Considered with many other features, these three families are not closer to each other than they are to any other group of monocotyledons (95).

On the other hand, closely related species may be assigned to different architectural models simply because some seemingly minor developmental switch causes changes that are strongly contrasted in the Hallé-Oldeman system. *Alstonia* spp. (Apocynaceae) are characterized by sympodial trunks, with each increment terminated by a whorl of sylleptic branches developed as the original apex aborts by parenchymatization (64). In *A. scholaris* (Prévost's model) the renewal shoot arises by prolepsis from a previously dormant lateral bud, just below the terminal tier. In contrast, in *A. macrophylla* (Koriba's model) the new trunk unit arises directly from an existing branch by re-erection (dedifferentiation) of an existing member of the terminal tier (30). When one considers the common suite of developmental features, which otherwise unites the two species, the physiological difference between the two methods of trunk substitution may not be trivial.

Architectural analysis makes phylogenetic interpretation more realistic. Paleobotanists must, of necessity, reconstruct the habit of the plants they study from fragmentary remains, and a knowledge of total organization of extant organisms provides a background to the reconstruction (20). There is a principle of "developmental uniformitarianism" that governs plant construction (and hence reconstruction) since vascular plants have similar mechanical and developmental constraints whether extant or extinct (86). Much of the diversity of tree organization represents contrasted methods of overcoming these constraints. The evolutionist must also recognize that phyletic change may affect different modular units in different degrees. An appreciation of the total developmental organization of a plant may demonstrate that existing reconstructions are unrealistic. For example, the original illustrations of the habit of the Devonian *Rhynia* (54) represent a habit seemingly impossible in a dynamic context. Niklas & O'Rourke (67) have appreciated this and suggested that growth habit can be the result of progressive collapse of axes under

their own weight, a process that occurs in a diversity of modern, unrelated taxa (e.g. *Lycopodium* sect. *Urostachya*; *Dieffenbachia* and related aroids; some herbaceous Labiatae).

In reverse, the paleobotanist may have recognized constructional principles that the neontologist readily overlooks, and sometimes the former may seem to have a better grasp of the importance of ontogenetic study (18). Eggert (22) first recognized that the progressive elaboration of shoot form (epidogenesis) and the subsequent progressive decline (apoxogenesis) in the arborescent lycopods (as measured largely by the amount and distribution of primary xylem) were of fundamental importance not only for the reconstruction of these plants but also for the analysis of modern plants.

Scheckler (82, 83) applied these principles in reconstructing the ultimate branch complex in the progymnospermous groups Aneurophytales and Archeopteridales; the application was based on the recognition that axes of different order can have different construction. The same principles need to be used in analyzing modern trees, which are usually also nonrecursive, i.e. their form is not the result of a single set of rules, repeated in each branch order. Shoot construction in the modern *Phyllocladus*, already referred to, has been homologized with that of *Archaeopteris* by Keng (53), but consideration of total organization, i.e. architecture, shows that similarities are quite superficial. Nevertheless, a comparison of *Phyllocladus* with *Archaeopteris* is useful architecturally in showing how the deployment of determinate and indeterminate phylloclades leads to crown construction. In *Phyllocladus*, indeterminate axes are of uniform construction, initially expressed as phylloclades, but are progressively fewer on progressively higher branch orders. In *Archaeopteris*, phylloclades are described as the ultimate determinate units of branch complexes with a highly apoxogenetic organization. These ancient trees offer problems of ontogeny not addressed in their reconstruction as adults; how, for example, was the initial photosynthetic apparatus organized in saplings? Establishing homologies in modular organisms is difficult when there are apoxogenetic and epidogenetic processes involved; it cannot be done without a complete architectural analysis. Morphologists have insufficiently addressed this question, which is unique to higher plants (81).

Many fossil plants seem highly deterministic in their organization, but this view may be the result of essentialist preconceptions dominating their reconstruction. Modern tree-like monocotyledons, common in tropical floras, provide instructive parallels. Features of their establishment growth as juveniles are retained in the adults because structures are not often obscured by secondary tissues and reiteration is limited. Even though the paleobotanist can compare plants from different stratigraphic levels, ontogenetic studies are only guesswork. For example, in comparing modern with ancient lycopods, one needs to appreciate how the massive erect axis of *Lepidodendron*, with its

first-order horizontal basal *Stigmaria*-axes, is generated from a narrow embryonic parent axis by some development of secondary tissue. This information is necessary when connecting these Carboniferous trees with the later plants like *Pleuromeia* and ultimately modern *Isoetes* (80). The example is illustrative of the way in which the architecture of descendant forms may have to be interpreted in terms of the juvenile phase of ancestors. This process of neotenus evolutionary development is often overlooked but probably holds the key to an understanding of much of the vegetative diversification of the higher plants. The approach in this example leads to the surprising conclusion that *Stigmaria*-axes are the product of the first dichotomy of the embryonic axis (80). Undoubtedly interplay between the results of the study of fossil and extant plants will mutually stimulate botanical areas that have too often been artificially disassociated.

Architecture and Ecology

The architectural approach to the analysis of plant form has resulted in a special classification (the models) that has little in the way of predictive properties, although it remains a valuable descriptive device. Functional attributes of different models need to be considered. It is unfortunate that the criteria used in the discrimination of architectural types are rarely understood at an adaptive level and may sometimes be simple correlates of each other, even when presented in a broadened context, as by Fisher (30, 32). Ecologists have therefore found little in ecological distribution that can account for the diversity of architectural models, even though it is claimed that frequent convergence of models among systematically unrelated groups must have a largely functional rather than a phylogenetic interpretation. Ashton (1) found a diversity of growth models in an analysis of trees in two sites in West Malaysia and emphasized that parameters such as leaf size, leaf area index, and leaf area density (quantitative parameters not considered in an initial architectural analysis) could be of more significance in ecological success than qualitative organization. Nevertheless, he points out that certain models (e.g. Tomlinson's, Leeuwenberg's) are rare in shady habits, whereas Troll's model (a very plastic type of organization) "is found in every conceivable tropical habitat within the ubiquitous Leguminosae." In contrast, it has been generally remarked that Attims's model is common in mangal (44). Here, one important defining parameter—that of continuous growth—may be fundamental, since continuous metabolism seems important in mangroves to maintain the salt-exclusion mechanism (93). The correlation is thus between habitat and one developmental feature. However, mangal is floristically impoverished, and the sample size is limited taxonomically.

Position of flowers defines some models and may represent the architectural expression of a suite of functional attributes. The two species of the

mangrove genus *Lumnitzera* (Combretaceae), i.e. *L. racemosa* and *L. littorea* (90, 93), represent Attims's and Scarrone's models, with contrasting lateral and terminal flowers, respectively. *Lumnitzera racemosa* has white, actinomorphic flowers and is pollinated by butterflies, which penetrate the canopy easily; *L. littorea* has red, somewhat zygomorphic flowers and is pollinated by birds, which do not penetrate the canopy easily. The architectural model here seems correlated with pollination biology, for the flowers are either within the canopy or at its perimeter. The relationship between architecture and reproductive biology is discussed in detail by Primack (72).

Efficiency of leaf display seems important in the ecological strategy of most species; nevertheless, architectural models are not usually defined by parameters that relate to photosynthetic efficiency. Tiered development of branches may minimize self-shading but can be a correlation of growth expression, as in Massart's model (monopodial trunk—rhythmic growth), and Prévost & Nozeran's model (sympodial trunk—substitution growth). Aubréville's model (the classical *Terminalia*-branching referred to earlier) provides a special case where deterministic plagiotropy by apposition growth can result in a highly regularized leaf display that has been shown to maximize photosynthesis by minimizing mutual shading between the rosettes of leaves born within each branch tier (35, 36, 37). Plagiotropy by apposition is frequently pronounced in tropical trees but not all exemplify Aubréville's model (in which plagiotropy is deterministic) in that many species exhibit opportunistic, i.e. nonarchitectural, apposition growth. *Bruguiera* and *Rhizophora* (both Rhizophoraceae) provide an instructive pair of genera growing in similar environments but contrasted in this way. *Rhizophora* (Attims's model) has *Terminalia* branching of an opportunistic kind and is very plastic in its organization (41); in *Bruguiera* (Aubréville's model), *Terminalia*-branching is deterministic. Plasticity in *Rhizophora* is facilitated by the stilt-like aerial roots.

This example again suggests that plasticity of organization rather than initial architecture may be the more significant adaptive mechanism. Nevertheless, a precise knowledge of architecture is a prerequisite to an understanding of the extent of reiteration, since the two processes of development are interdependent. The change of architecture (or architectural parameters) with age, as discussed earlier, becomes understandable in the forest environment, since a tree that finally reaches the canopy and even emerges from it must experience a contrasted set of micro-environments as it grows from seedling to maturity. Again, what is architecture (deterministic) in one species may be reiteration (opportunistic) in another. It is frequently recognized that some of the more tightly programmed of the Hallé-Oldeman models are characteristic of the forest understory (44). Here architecture may be directly adaptive. However, as Oldeman (69) emphasizes adaptation is a relative concept. A

sapling designated as "suppressed" by a forester because it expresses only a limited set of its architectural attributes may be equally adapted as an understory treelet with a fully elaborated growth model. The suppressed sapling, surviving in the understory, may have a greater growth potential (as a tree of the future) if the light intensity is increased abruptly by a gap created by a tree fall. In contrast, a tree fully adapted to limited light may be incapable of further growth and incapable of using increased light levels. Kahn (52) suggests that the ecological distribution of the trunkless habit in palms (a species-specific character implicating size) is determined by the size of the forest gap and the way in which it closes. Small gaps close more rapidly, resulting in light insufficient to sustain trunk growth; acaulescent forms are thus selected.

It is for these reasons that the simple designation of architecture as "adaptive" is inappropriate without due consideration for the circumstances under which a plant grows. Architecture and ecology are nevertheless intimately interdependent.

Architecture and Simulation

Precise architectural analysis is initially qualitative but provides basic information that allows quantification. Relevant parameters such as branch length and branch angle (which are a minimum requirement for the description of tree-like forms; 47) can be extracted from real trees, or a branch complex, and represented by a simple stick diagram. These in turn are manipulable by computers as stereo and rotatable images in three dimensions. Attempts at reality introduce appendages as well as axes (73). Modelling trees realistically is very complex because of the nonrecursive (nonstationary) design of most trees; programs that take into account architectural changes are not often attempted because they can exceed the capacity of quite large computers. They are possible, however, if the "rules" in real trees are well understood (9, 74, 75). In another direction a problem-solving approach will test a hypothesis, such as the question of how minimum mutual shading (which presumably maximizes photosynthesis) is achieved. This has been done most extensively with *Terminalia catappa*, our archetypical "tropical tree," by Fisher & Honda (34, 35, 36). These studies are exemplary because they eventually compare information from theoretical computer-drawn trees with data from 32 species of real trees (33, 37). The interaction of branch complexes originating from different trees is an important process in competition within the forest and has been studied in a preliminary way by simulation (48). Simulation may be useful simply to confirm an existing description or analysis when real and simulated trees resemble each other closely (40, 49).

A preliminary analysis of flow rates has been modelled, showing how the form of the tree may be determined by the relative distribution of nutrients, growth substances, or even water between parent axis and branch (48).

Curiously, one set of rules (49) generated a series of artificial examples that were subsequently shown to occur in the real tree *Tabebuia rosea* during its period of asymmetric growth (11). The hypothesis that the manipulation of flow rates in the real tree is the same as in the simulated tree (9) can only be verified by experimental observation. Simple techniques for doing this already exist, and they are explained below. The significance of modelling, in principle, is that it allows one to manipulate values and produce preliminary results that otherwise could only be obtained from many years of field experiments. Therefore, modelling is most useful in the design of experiments on real trees and as an indicator of the parameters significant in the control of tree form or of the adaptive significance of existing form. Modelling has been used to quantify crown shape as branch orders increase and so to demonstrate that branch ratios can change with age (10, 49). This is a direct expression of the nonrecursive nature of tree growth.

Rhizomatous plants lend themselves to simulation because they have precise organization, grow in one plane, and have unlimited capacity for spread, because they are not self-supporting. Modelling allows the population biology of their clonal spread to be simulated over many generations (4, 6). Once the deterministic "rules" of clonal growth have been established by field analysis, opportunistic aspects of architecture can be simulated. Examination of a wide variety of rhizomatous plants shows major contrasted "strategies" of clonal spread which are a simple expression of basic differences in the distribution of meristems in the rhizomatous portion of the plant body (7). Rhizome strategies that are deterministically linear and involve branching only as an opportunistic process may be contrasted with deterministically branched systems (5); however, opportunistic processes can partly or wholly obscure the original geometry (16). Meristem distribution is usually thought to be determined directly by phyllotaxis, but growing numbers of examples show that the phyllotactic "rules" are transcended by the nonconformable redistribution of meristems. The meristem that forms the renewal shoot may be "rotated" from its normal axillary position, as in species of *Costus*, *Heliconia* (J. LaFrankie, unpublished observations), *Medeola* (3), and *Maianthemum* (*Smilacina*) (56, 57). The morphological basis for clonal growth is being investigated increasingly in temperate ecology, but rhizome morphology has been little investigated in tropical forests. However, when one considers the abundance of rhizomatous epiphytes and root-climbing plants, the scope for further investigation remains large.

Architecture and Morphogenesis

Architectural studies of tropical plants have demonstrated that current notions of organizational control in plants need amplifying on the basis of information from a sample size much larger than is available in temperate floras. In addition, many correlations that require explanation in morphogenetic terms

have been revealed. The nonrecursive nature of much tree organization is a direct expression of branch differentiation. For example, apical dominance is not a universal feature of branch control in tropical trees; many of them branch wholly or partly by syllepsis (the synchronous development of parent and branch axis). This is in contrast to the almost universal prolepsis (nonsynchronous development of parent and branch axis) which characterizes most north temperate trees. [Shrubs are a distinctive exception; the difference between sylleptic and proleptic shoots is important in shoot organization of the rose (105).] The reason for the generalized geographic contrast has not been found. Architectural analysis demonstrates a fairly consistent correlation between trunk-branch synchrony and symmetry. Sylleptic branches tend to be plagiotropic, and proleptic branches tend to be orthotropic, although Mueller (64) emphasizes that these correlations are not absolute. The correlation is best demonstrated in species belonging to a number of architectural models with strong contrast between the two kinds of axis; the contrasting axes lead to a very precise crown form. For example, Nozeran's model, exemplified by cocoa (*Theobroma cacao*), produces a series of sylleptic plagiotropic branch tiers, each tier being the terminal product of growth of an orthotropic axis, itself produced earlier by prolepsis from a previously dormant meristem just below the previous tier. Meristems that originate by syllepsis versus prolepsis produce morphologically distinguishable kinds of leaves with contrasted phyllotaxis (distichous versus spiral) and differences in subsequent branching pattern (100). However, the situation is complicated because leaf axils support two kinds of buds, principal and subordinate, so many combinations are possible between meristem type, chronology of development, type of parent shoot, and type of daughter shoot. The only consistent correlation seems to be that subordinate buds on both orthotropic and plagiotropic shoots are the sources of inflorescences, while principal buds, on both orthotropic and plagiotropic parent axes, are always plagiotropic. Principal buds that develop by prolepsis usually form a shoot whose symmetry conforms to that of the parent axis. In species other than cocoa, the exclusive branching process in many model-conforming trees is by syllepsis; proleptic development of a meristem results in reiteration (usually of a trunk axis).

The division of labor implied in these structural contrasts is inherent in the construction of all lateral meristems in woody plants, since at initiation there is usually an initial dorsiventrality imposed by the arrangement of prophylls in a horizontal plane. If the lateral meristem grows out without rest (syllepsis), the dorsiventrality seems to be maintained. Meristems that undergo some period of rest before they grow out (prolepsis) can make the transition to radial symmetry (e.g. spiral phyllotaxis) while in the resting condition (101).

Structural contrasts between sylleptic and proleptic branches at their level of insertion remain little investigated. However, sylleptic branches have a

much broader pith connection and can have a much more extensive primary vascular connection than proleptic branches (101). The presence of a pith discontinuity along a trunk can be used to identify previous sympodial displacement of a leader, as in *Tsuga* (46). It is of value to understand the time at which a lateral meristem becomes "fixed" in its future developmental organization. In *Myrsine*, where there is only one bud per leaf axil, differentiation is early (101). The situation is rendered more involved when a bud complex produces different meristems with contrasted developmental potential at a single node. A study by Wheat (102) of mangrove Rhizophoraceae suggests that position within the linear series of a single branch complex determines orientation.

The field for experimental manipulation in studies of branching processes in tropical woody plants remains quite unexplored. It is clear from numerous descriptive studies that small developmental shifts can produce marked morphological differences especially where the distinction between deterministic (architectural) and opportunistic (reiterative) aspects of crown development is not very clear. Shifts in the concentrations of growth substances undoubtedly are involved, and experimental perturbation of natural hormone levels could indicate the nature of underlying morphogenetic processes. It is also a reasonable assumption that differentiation of axes is determined by distribution of growth substances. There is a larger gap between our knowledge of how biochemical control of form is achieved and the evident complexity in crown construction. Architectural analysis has certainly been helpful in making clear that complexity.

Hydraulic Architecture

Since the xylem conduits in woody plants are dead cells, water flow is governed directly by physical processes. How then does the tree control the distribution of water in such a way that distal or uppermost modules receive water preferentially, even though they are at the greatest hydrostatic disadvantage because of their height or greater path length (with implied greater resistance)? We may similarly ask how water can be distributed unequally in a branch complex or among different kinds of branch connection. Some kind of "hydraulic dominance" must exist. This subject has been approached by M. H. Zimmermann (107) who has provided experimental evidence for differential resistance to flow at branch junctions when these are compared with interbranch regions (106). The generalized concept is that the "constriction hypothesis" accounts for localized impedance. An analogy would be between the tree and an electric or plumbing circuit which has sets of resistors or valves to control the flow of electrons or water. Niklas & Banks (66) suggest that the early differentiation of vascular plants may have involved such differential impedance at branch forks. It must be remembered that under

conditions of transpiration water moves in plants under negative pressures and that a physical limit to the tension that can be accommodated by xylem elements is set by the tensile strength of water. When an upper limit (which may not be constant) is exceeded, the water column cavitates (i.e. vaporizes) and an embolism, contained by the pit structure of tracheary elements, is created. Refilling of embolized elements (by positive pressures) then becomes an important process, also controlled by cellwall structure (84, 85).

Evidence to support the constriction hypothesis comes from lower values for leaf-specific conductivity (xylem conductivity related to the weight of total leaves supplied) at branch junctions. Values have so far been obtained only for a few temperate trees and conifers (24, 25, 106). Palms provide good material for experimental study because they are structurally simple, with a fixed crown size and a fixed vascular system whose detailed construction is well known (108). They have provided anatomical and experimental evidence to support the constriction hypothesis, since there is a pressure drop at the leaf insertion, which is correlated with the narrow diameter of xylem elements (all protoxylem) in the leaf trace attachment (84, 85, 109). Sperry and Zimmerman make an important distinction between the vascular leaf insertion (the internal insertion of leaf protoxylem strands on the stem metaxylem elements) and the morphological leaf insertion (the superficial or topographic insertion of the leaf base). Development of the vascular system in the palm crown is a highly integrated process which generates this functionally important anatomy (94). The structural basis for hydraulic constrictions in conifers and dicotyledons may also relate to differences in tracheary element diameter and number (e.g. 24, 25).

Tropical woody plants with their diversified methods of developing contrasted types of branch complexes provide ample examples for comparative experimental and developmental study. *Terminalia*-branching again offers itself as a subject for investigation, since the regular eviction of terminal by lateral meristems determines overall construction. Preliminary measurements do not show a very regular pattern of flow rates contrasting the supply to short shoots vs that to the long (J. Zakrzewski, unpublished).

Considerations of hydraulics and development may offer an explanation for syllepsis if vessel differentiation is continuous from branch to parent axis in sylleptic but not proleptic axis unions, for which there is limited evidence. Continuous vessels might result in embolisms being "shared" between parent and daughter axis in the former, but not the latter kind of union. In cold or seasonal climates, the spread of embolisms might be more detrimental to the maintenance of crown form, and the elaboration of diversified architectures might be inhibited. These ideas are, of course, highly speculative but suggest how approaches that integrate development, structure, and function are needed in the understanding of tree architecture.

Topographic and hydraulic dominance have been shown to be correlated in conifers. Ewers & Zimmermann (24, 25) showed a large difference in leaf-specific conductivity between leader and uppermost branches in *Abies*, which is strongly monopodial, but a small difference in *Tsuga*, which is weakly monopodial (46). These differences are also correlated with habitat differences. *Tsuga* in particular is a shade tolerant tree, subject to mechanical damage; opportunistic leader development may be valuable.

Architecture and Mechanics

Trees are self-supporting structures with wide mechanical safety margins (63). Simple allometric relations between height and diameter have been used to determine factors that may control crown form in relation to mechanical success. Trees are not geometrically self-similar, i.e. do not retain a linear proportion between height and diameter. Rather they retain elastic self-similarity, maintaining a constant bending moment that is expressed as a proportionately greater increase in diameter than in height with age. This result is generally assumed to be a consequence of the uniform properties of wood. However, other kinds of allometric relationships are likely to exist and may be determined by the architecture, anatomical properties, and successional status of a species. Late successional canopy trees have been shown to have a wider margin of safety than early successional species (79).

King (55) measured the applied crown load needed to bend over understory treelets in tropical lowland forest in Costa Rica in order to provide a measure of the margin of safety against elastic instability. He found low safety factors and interpreted this as allowing understory plants to attain greater height for given support cost, even though mechanical failure would be more likely to occur. His samples include two palms, plants in which architecture is distinctively correlated with anatomy—notably the absence of secondary thickening.

Theoretically, palms should be vastly overbuilt because their early ontogeny must anticipate future mechanical demands that increase with age and height, i.e. the diameter should remain constant with height. Measurements show that the proportions vary in different species (77). Some species show a relationship that approximates that of dicotyledonous trees because there are unique methods of secondary expansion by means of enlargement of ground parenchyma cells in a way that does not disrupt the vascular system (78). The most dramatic difference between many palms and more conventional trees is that there can be progressive change in the mechanical properties of supporting cells with age. Cell walls, notably those of the vascular bundle fibers, become thicker and increasingly more lignified so that the Young's modulus (stiffness) of the axis progressively increases as the palm grows taller (77). Palms owe part of their ecological success to this

minimization of the anticipatory overbuilding process. The developmental process underlying these mechanisms is cytologically distinctive, because the cytoplasm of the fiber retains a capacity for cell wall deposition that extends over many years. Palm leaves have been found suitable subjects for mechanical analysis because their angle of inclination relates directly to photosynthetic efficiency (14, 15).

Secondary changes in stem construction that relate to changes in mechanical properties with position are, of course, familiar in the distribution of reaction wood in both dicotyledons and conifers. Such changes are implicated in at least two architectural models, those of Koriba and Troll. A study of the distribution of reaction wood in tropical trees, in relation to their architecture shows that reaction anatomy is less significant in some species than superficial observation would suggest (39). *Terminalia* has proved useful for experimental studies of induction of reaction anatomy because its architecture is so well known (31); it is the first tropical example to be so investigated. Mechanisms for reorienting axes, both in a deterministic and an opportunistic mode, may be quite diverse. Fisher & Mueller (38) suggested that the distinctive fiber distribution within the secondary phloem of some dicotyledons, by inducing internal tensions, could be mechanically beneficial in reorientating axes or maintaining axis stability in the absence of reaction wood. The phenomenon of phloem dilatation has been known to plant anatomists for many years (23). Putting it into a mechanical context will require architectural analysis.

Other Aspects

The previous sections have given an indication of some of the directions in which architectural analysis has proceeded since its inception in 1970. Space does not permit an equally detailed treatment of several other relevant topics that can be mentioned, albeit briefly. At a practical level, architecture and crop management are intimately related (97). Many tropical crop plants are trees; crop production may be continuous or periodic, a feature that may have architectural foundations. Mango (Scarrone's model) contrasts with coconut (Corner's model) as an extreme example. Seasonal production of mangos is immediately determined by terminal inflorescences and the method of shoot substitution. Coconut is indeterminate and evergrowing, not only emblematic of the tropics, but representing a suite of constructional features utterly unknown in temperate trees.

Plant demographers can quantify architecture in a distinctive way by treating a tree as a population of meristems, to be studied in terms of a banking account, with capital inflow, loss, and stock "on deposit," all fluctuating under the influence of organizational and environmental factors. Meristems (buds) can be counted, their functions (e.g. active versus inactive)

assessed, and changes in time observed directly. Reproductive effort comes to have an architectural component, because, as we have seen, architecture can be defined by the position and number of reproductive meristems (flowers, seeds; cf. 72). Maillette (61, 62) in her analysis of *Betula pubescens* provides an example of this approach (cf. 104). Extensive reviews of these approaches already exist (e.g. 99, 103, 104).

CONCLUSIONS

This discussion has ranged over many disciplines, with the objective of presenting plant architecture as a central topic with extensions into fields too often kept separate from each other. In reviewing Hallé & Oldeman's initial presentation (89) I described it as a major contribution to plant morphology. I was correct only in the sense that plant morphology is an integrative discipline, as this review attempts to demonstrate, rather than a subject restricted to the comparative study of the anatomical details of plant life cycles. In this sense, architecture belongs more rightly within the fields of plant ecology and plant demography. If one accepts a broad approach, plant morphology is then seen as a lively and thriving discipline, albeit encapsulated in the pages of journals like the *Journal of Ecology* and *Ecology*, a conclusion that might surprise their editors. The extent of Hallé & Oldeman's contribution is then best seen by the fact that I have been able to include only a very limited coverage of the subject.

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